A PHYLETIC STUDY OF THE LAKE TANGANYIKA CICHLID GENERA *ASPROTILAPIA, ECTODUS, LESTRADEA, CUNNINGTONIA, OPHTHALMOCHROMIS,* AND *OPHTHALMOTILAPIA*

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CONTENTS

ABSTRACT. On the basis of comparative osteology and myology, *Asprotilapia, Ectodus, Lestradea, Cunningtonia, Ophthalmochromis,* and *Ophthalmotilapia* of Lake Tanganyika are hypothesized to be members of a monophyletic lineage of cichlid fishes. All members share the following suite of characters: (1) the entopterygoid is widely separated from the palatine; (2) the posterior and dorsal margins of the palatine form a 90° angle; (3) the slender hyomandibula has a long symplectic process and a very reduced hyomandibular flange; (4) the anterior margin of the pterosphenoid is notched; (5) the vertical depth of the metapterygoid is shallow; (6) the operculum has a distinct auricular process; (7) the transversus dorsalis muscle is reduced; and (8) the obliquus posterior muscle is enlarged. These characters are considered specialized when compared with the accepted generalized morphology of *Astatotilapia.* The phyletic relationships of this lineage are documented by synapomorphies that distinguish subunits of decreasing levels of universality within the assemblage. *Asprotilapia* represents a highly specialized branch with six major skeletomuscular specializations. The remaining five genera are pictured as a second lin-

eage, of which *Ectodus* is the most generalized taxon. On the basis of recency of common descent, *Ophthalmochromis* is synonymized with the genus *Ophthalmotilapia.* Although there is no doubt that the *Ophthalmotilapia* lineage has undergone extensive morphological radiation in both skull structure and dentition, the data on morphology, function, trophic ecology, and behavior of this and other cichlid lineages have failed to establish unequivocally that the morphological radiation is also adaptive. The morphological and functional pattern in this lineage reinforces the paradox that morphologically and phylogenetically most specialized cichlid taxa are not only remarkable specialists but also jacks-of-all-trades.

INTRODUCTION

The precise phylogenetic interrelationships of the endemic cichlids in Lake Tanganyika are still unknown (e.g., Fryer and Iles, 1972: 507). Essentially the problem is to distinguish groups that are true, hierarchically evolved sister groups showing increasing specialization or apomorphy, from groups that are gradal assemblages of polyphyletic ancestry (Greenwood, 1974, 1979). Liem and Stewart (1976) have shown that the lepidophagous cichlids of Lake Tanganyika represent a monophyletic lineage. Recently Liem (1979) has postulated that because of the basic homogeneity in specialized morphology and function, the invertebrate picking cichlids of Lake Tanganyika must have originated from a common ancestor. Greenwood (1979) has synonymized *Limnotilapia* with *Simo-*

chromis to show the close phyletic rela-
tionships of two genera previously pic-
tured as belonging to two different
lineages (Fryer and Iles, 1972: 507). A
complete analysis of phyletic relation-
ships for the endemic cichlids is hin-
dered because of an apparent absence of
synapomorphic features which would en-
able one to build up the various levels of
relationship, and a phyletic analysis of
cichlids from other lakes and rivers. This
paper is part of a series dealing with the
establishment of monophyletic lineages.
Such an attempt represents a first step to-
ward the ultimate goal of interrelating
the different lineages on a sister group
basis.

This paper deals with six endemic gen-
era of Lake Tanganyika: *Asprotilapia,*
Boulenger, 1901; *Ectodus,* Boulenger,
1900; *Lestradea,* Poll, 1943; *Cunningto-
nia,* Boulenger, 1906; *Ophthalmotilapia,*
Boulenger, 1901; and *Ophthalmochro-
mis,* Poll, 1956. Except for *Ectodus,* this
assemblage is characterized as predomi-
nantly herbivorous, inhabiting rocky hab-
itats of Lake Tanganyika down to a depth
of 15 m. *Ectodus* is especially abundant
in shallower and sandy habitats. With the
exception of *Ectodus descampsi,* all
members of the group possess long intes-
tinal tracts (2.5–6 times the standard
length) and exploit filamentous and uni-
cellular algae, diatoms, crustaceans, and
insect larvae as food sources. Based on
comparative osteological and myological
data, I am presenting a hypothesis that
the assemblage is monophyletic, with
Asprotilapia as a very specialized form,
and *Ectodus* and *Lestradea* as the least
specialized representatives.

In this study only a limited number of
functional data have been gathered from
Lestradea and *Ophthalmotilapia.* How-
ever, much information from other cich-
lids (Liem, 1978, 1979, 1980) can be ap-
plied to this lineage in determining the
nature and possible evolutionary direc-
tion of the character complexes. A pro-
visional phylogenetic scheme is pre-
sented as a hypothesis, with each branch

defined by its unique morphological spe-
cializations.

MATERIALS AND METHODS

Osteological studies are based on aliz-
arin preparations and some dried skele-
tons. Osteological nomenclature follows
Liem and Stewart (1976) and Barel *et al.*
(1976). The myology has been studied
from formalin fixed specimens, which are
stored in 70% ethyl alcohol. With very
few exceptions the nomenclature of Win-
terbottom (1974) and Anker (1978) is fol-
lowed. All drawings were made by
means of the Wild-M5 camera lucida.

The following specimens from the Brit-
ish Museum (BM) and the Museum of
Comparative Zoology (MCZ) have been
studied:

Asprotilapia leptura BM 1906.9.6.157
Asprotilapia leptura BM 671 (dried skeleton)
Aulonocranus dewindti BM 1960.9.30.4642–4656
Aulonocranus dewindti MCZ 49305
Callochromis macrops BM 1960.9.30.2821–2823
Callochromis melanostigma BM 1960.9.30.2845–
    2859
Callochromis pleurospilus MCZ 49280
Cardiopharynx schoutedeni BM 1960.9.30.1574–
    1615
Cunningtonia longiventralis MCZ 49243
Cunningtonia longiventralis BM 1960.9.30.1912–
    1919
Ectodus descampsi BM 1961.11.22.113–119
Grammatotria lemairei MCZ 49277
Grammatotria lemairei BM 1960.9.30.3317–3330
Astatotilapia ("Haplochromis") burtoni BM
    1960.9.30.2415–2433
Lamprologus elongatus BM 1960.9.30.6790–6793
Lamprologus elongatus MCZ 49251
Lamprologus moorei MCZ 49245
Leptochromis calliurus BM 1960.9.30.3351–3353
Lestradea perspicax perspicax BM 1960.9.30.1468–
    1484
Limnochromis auritus BM 1960.9.30.1981–1985
Ophthalmochromis nasutus MCZ 49232
Ophthalmochromis ventralis BM 1960.9.30.1689–
    1694
Ophthalmochromis ventralis MCZ 49232
Ophthalmotilapia boops BM 1960.9.30.1720–1724
Ophthalmotilapia boops BM 1960.9.30.1716–1718
Sarotherodon nilotica MCZ 49312
Trematocara unimaculatum BM 1961.11.22.519–
    528
Trematocara unimaculatum MCZ 49262
Tylochromis polylepis BM 1960.9.30.109–113
Xenotilapia ornatipinnis MCZ 49266
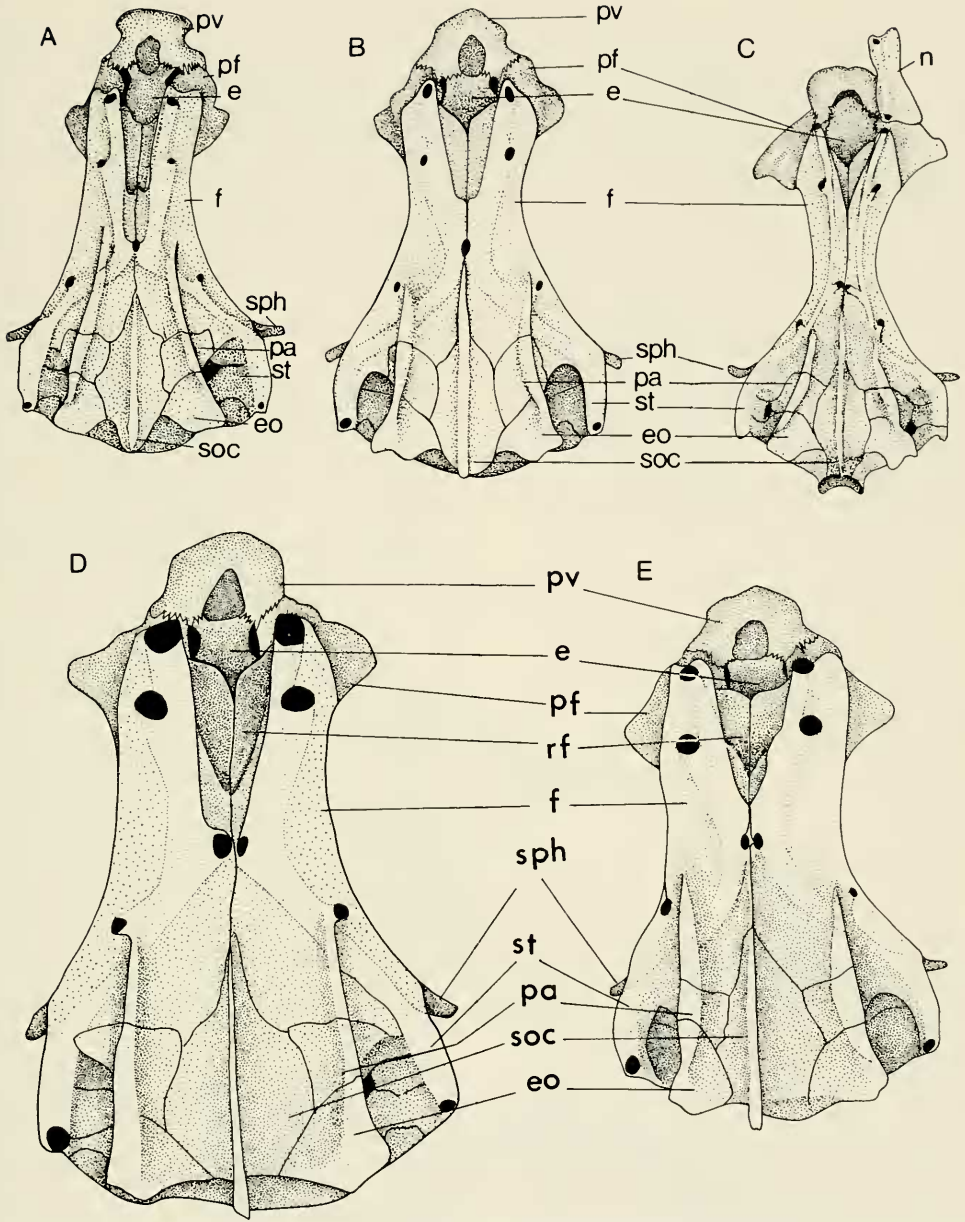*Xenotilapia sima* BM 1961.11.22.208–211

Figure 1.   Dorsal aspect of the neurocranium. A, *Ectodus descampsi*; B, *Lestradea perspicax*; C, *Asprotilapia leptura*; D, *Ophthalmotilapia ventralis*; E, *Ophthalmotilapia boops*.

OSTEOLOGICAL ASPECTS OF *ECTODUS*

The neurocranium of *Ectodus* retains many primitive features found in *Astatotilapia* ("*Haplochromis*") *burtoni* and *A. elegans* (Liem and Osse, 1975; Barel et al., 1976), such as the somewhat decurved dorsal profile to the preorbital face and the high cranial vault. However, the ethmovomerine region is relatively
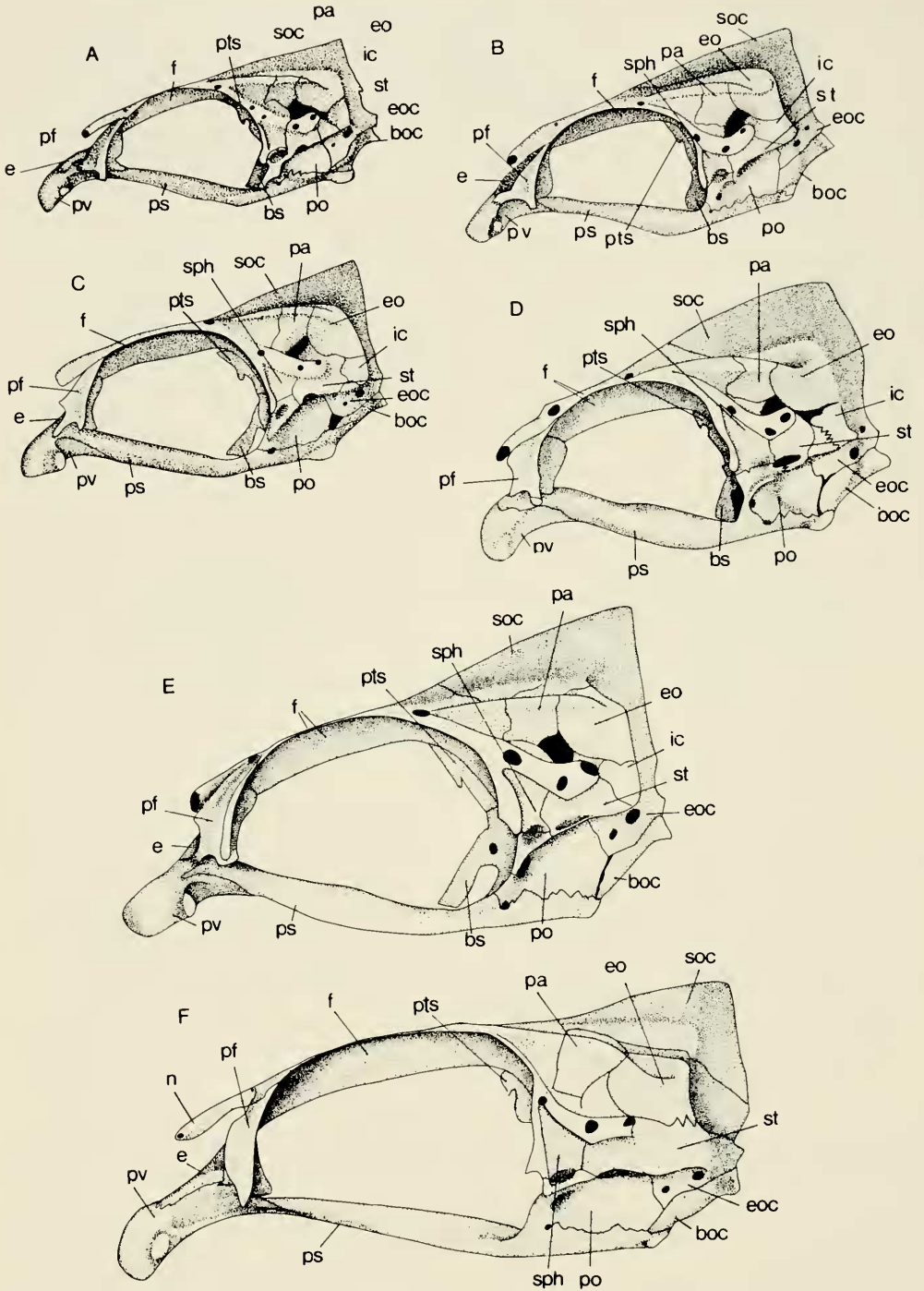
Figure 2.   Lateral aspect of the neurocranium. A, *Ectodus descampsi*; B, *Lestradea perspicax*; C, *Cunningtonia longiventralis*; D, *Ophthalmotilapia boops*; E, *Ophthalmotilapia ventralis*; F, *Asprotilapia leptura*.

long and is dorsally differentiated into a well-developed rostral fossa, which is made up by the ethmoid and the depressed anteromedial wings of the frontals (Fig. 1A:e,f). The ethmoid is suturally united with the ascending processes of the vomer and with the lateral ethmoids (Fig. 2A:e,pf). The long axis of the basioccipital makes a 60–70° angle with that of the parasphenoid (Fig. 2). Both the basioccipital and parasphenoid bones contribute to the formation of a prominent pharyngeal apophysis, which is therefore of the "*Haplochromis*" type. Another specialization can be found in the pterosphenoid in the form of a deep notch in the anterior margin of the pterosphenoid (Fig. 2A:pts). The saccular bulla is greatly enlarged (Figs. 2A, 3A).

Morphologically the suspensory apparatus of *Ectodus* deviates from the more generalized configuration of that in *Astatotilapia burtoni* (Fig. 4A; Liem and Osse, 1975). The hyomandibula is slender with an elongate symplectic process and a much reduced flange area below the anterior condyle. The two hyomandibular condyles are distinctly separated, while the symplectic process is connected to the metapterygoid, which is a characteristically shallow bone. The reduced entopterygoid is separated from both the ectopterygoid and the palatine. Half of the entopterygoid's lateral surface is overlapped by the quadrate. The palatine bone is unusual in having its posterior and dorsal border meet at a 90° angle. Posteriorly the suspensory apparatus is delineated by a large preoperculum of which the outer rims of the horizontal and vertical limbs make a distinct 90° angle. The anterior border of the suspensory apparatus formed by the ectopterygoid and the palatine is oblique, making a 60° angle with the horizontal plane.

The jaw apparatus in *Ectodus* (Fig. 4A) possesses a generalized premaxilla resembling that of *Astatotilapia burtoni*, but the maxilla has a prominent earlike postmaxillary process. The elongate, slender mandible is characterized by

large, widely separated ascending processes of the dentary and anguloarticular. The ascending process of the anguloarticular is expanded posteriorly to form an adductor fossa, serving as the insertion site of the A_2 part of the adductor mandibulae muscle complex (Fig. 6A:am_2).

The size, shape, and configuration of the opercular apparatus (Fig. 5A) do not differ from those of generalized cichlids. In *Ectodus* the posterodorsal corner of the operculum is raised to form an auricular process, which is not encountered in generalized cichlids.

Of the well-developed five or six circumorbitals, the large lacrimal is distinctly shaped and possesses six sensory pores (Fig. 5A:la). The ventral margin is convex, while the posterodorsal margin is concave. The anterodorsal margin is straight. Anteriorly the lacrimal ends in an anteriorly directed angular process.

The branchial skeleton is not described here because the elements retain a relatively generalized condition and do not contribute to the solution of phylogenetic relationships in this group of cichlids.

MYOLOGICAL ASPECTS OF *ECTODUS*

The lateral head muscles of *Ectodus* (Fig. 6A) retain their unspecialized condition in respect to topography, configuration, and structure. Thus the description of the head muscles of *Astatotilapia elegans* by Anker (1978) also applies to those of *Ectodus*. The adductor mandibulae complex (A_1, A_2, A_3, A_w) of *Ectodus* is identical to that of *A. burtoni*, except that the muscle fibers in the former are considerably more elongate, a feature which is probably correlated with the much larger orbit and the longer and more shallow suspensory apparatus. The levator arcus palatini in *Ectodus* (Fig. 6A:lap) is less voluminous than in *A. burtoni* (Liem and Osse, 1975). Because the hyomandibular flange zone is much more restricted, most of the fibers insert on the

muscular process of the metapterygoid. The other lateral head muscles have not undergone any specialization and will not be described here (Fig. 6A:aap,do,lo,ep).

The ventral muscles of the head of *Ectodus* (Fig. 7A:gh,sh) do exhibit several specializations if compared with those of *A. burtoni* and *A. elegans*. The left and right geniohyoideus anterior (Fig. 7A:gha) are clearly separated, cylindrical muscles, each attaching to the dentary near the mandibular symphysis ventral to the small parallel-fibered intermandibularis. A transverse myosept interrupts the fiber course of the geniohyoideus just anterior to the hyoid symphysis. From the transverse myosept, the geniohyoideus posterior runs laterally to attach to the lateral aspect of the hyoid above the first 2 branchiostegals. The hyohyoideus complex (Fig. 7A:hhs,hhi) lies between the hyoids, the branchiostegals and the medial aspect of the opercular apparatus. We may distinguish three parts: (1) the hyohyoideus inferior (Fig. 7A:hhi) arising from the anteroventral corner of the hyoid ramus runs caudally and slightly lateral to insert on the first to fourth branchiostegal rays by splitting into four heads; (2) the hyohyoideus superior (Fig. 7A:hhs) runs between the rays and the medial aspect of the gill cover; and (3) the hyohyoideus transversus (Fig. 7A:hht) runs between the first left and first right branchiostegals. The hyohyoideus transversus is much better developed than in *A. burtoni*.

In the branchial musculature, the ventral muscles correspond with those of more generalized cichlids (e.g., *Astatotilapia elegans*, Anker, 1978) with respect to topography, structure, attachment sites and shape. Therefore, the description here will be focussed mainly on the dorsal muscles (Figs. 7A, 8A).

Both the levatores externi and interni (Figs. 7A, 8A:le,li) originate from the muscular process of the prootic. The levator internus 1 (or anterior) runs medially and ventrocaudally towards the junc-

tion of pharyngobranchials 2 and 3, inserting on both bones. Levator internus 2 (or posterior) passes ventrocaudally along the outer margin of the second pharyngobranchial to insert on the third pharyngobranchial near the junction of the third and fourth epibranchials. The levatores interni are equally developed, cylindrical muscles. The levatores externi 1–3 are relatively slender, straplike muscles running caudoventrally to insert on the dorsal aspects of the epibranchials 1–3 respectively. As in all cichlids (Liem, 1974), the fourth levator externus is the dominant component of the externi complex, lying in a parasagittal plane. Its fibers pass ventrally to converge on the muscular process of the lower pharyngeal jaw. The insertion appears as a complex mixture of muscular and tendinous elements. Only a few lateral fibers attach to the dorsal side of the fourth epibranchial by means of an aponeurotic plate.

The obliquus posterior muscle (Fig. 8A:obp) is characteristically a highly developed muscle in *Ectodus* originating from the dorsal surface of the fourth epibranchial. From this expanded origin, the fibers run laterally and caudoventrally converging on the muscular process of the lower pharyngeal jaw. The insertion site is medial and ventral to that of the fourth levator externus.

Joining the insertion sites of the fourth levator externus and obliquus posterior muscles on the muscular process of the lower pharyngeal jaw is the fifth adductor muscle (Fig. 8A:ad). This spindle-shaped muscle attaches to the medial surface of the dorsal end of the shank of the fourth epibranchial adjacent to its articulation with the fourth ceratobranchial. From this point, the muscle runs ventrally to the muscular process, to which it attaches laterally and posteriorly to the insertion site of the fourth levator externus.

The two transversi dorsales muscles in *Ectodus* (Fig. 8A:tda,tdp) have undergone a reduction as compared with those of *Astatotilapia elegans* (Anker, 1978). Basically, the transversi dorsalis anterior

muscles run between the second pha-ryngobranchials and the second epibran-chials. The drastically reduced transver-sus dorsalis posterior is a small, straplike muscle which runs between the left and right fourth epibranchials. The fibers run without interruption between the two at-tachments. As in more generalized cich-lids, the transversus dorsalis anterior, al-though reduced in *Ectodus*, is differentiated into four heads (Anker, 1978). The posterior head (M. transversus epibranchialis 2 pars dorsalis) arises mus-culously from the dorsal surface of the anterior fork of the second epibranchial and runs medially over the second pha-ryngobranchial towards a large aponeu-rosis. Very closely associated with the posterior head is a more ventrally located component (M. transversus epibranchia-lis 2 pars ventralis) with its attachment to the junction of the second pharyngobran-chial and second epibranchial and con-necting with the median aponeurosis. The third head (M. transversus pharyn-gobranchialis 2) is the anterior one, run-ning between the rostromedial surfaces of the left and right pharyngobranchials. Finally, the fourth head (M. cranio-pha-ryngobranchialis 2) arises from the neu-rocranium just anterior to the articulation with the first pharyngobranchial, and runs posterolaterally and ventrally to in-sert on the lateral edge of the anterior as-pect of the second pharyngobranchial.

The obliquus dorsalis muscle (Fig. 8A:od) originates from the area lateral to the pharyngeal apophysis of the third pharyngobranchial and runs caudolater-ally to insert on both the dorsal aspect of the third epibranchial just medial to the insertion site of the third levator externus and the anterodorsal aspect of the fourth epibranchial.

The large retractor dorsalis muscle (Fig. 8A:rd) runs parasagittally close to the medial plane. Its extensive origin is from the exoccipital, the vertebral bodies of the first three vertebrae, and the apophysis of the third vertebra. From these points, the fibers run anteroven-trally to insert musculously on the pos-terodorsal surfaces of both the third and fourth pharyngobranchials.

Three ventral muscles, the pharyngo-hyoideus and the pharyngocleithralis ex-ternus and internus, play an important role in the operation of the lower pharyn-geal jaw (Liem, 1974, 1978). Although none of the three muscles (Fig. 7A:ph,pci,pce) exhibits morphological specializations which can be used in a phylogenetic analysis, they will be brief-ly described as a basis for future, more functionally focussed studies. As in most cichlids, the fibers of the pharyngohyoi-deus are interrupted by an aponeurotic sheet halfway along the length of the muscle. Anteriorly, the muscle attaches to the urohyal. Near this insertion site, the left and right pharyngohyoideus merge inseparably into one unit. Poste-riorly, the muscle fibers blend into a strong tendon attached to the lateral sur-face of the anteroventral portion of the lower pharyngeal jaw. The pharyngo-cleithralis externus arises from the an-terolateral surface of the cleithrum from nearly the ventral tip and dorsally until about one-third of its vertical depth. From this origin, the fibers run in a par-allel fashion dorsally and slightly ante-riorly converging on an aponeurotic sys-tem which merges with the insertion tendon of the pharyngohyoideus. How-ever, a subdivision of this aponeurotic system takes up a more lateral course to attach on the fourth epibranchial. The pharyngocleithralis internus originates from a fossa to a point about midway on the vertical depth of the cleithrum; its fi-bers run anteroventrally to converge on a tendon which inserts on the lower pha-ryngeal jaw just medial and posterior to the insertion site of the pharyngohyoi-deus muscle.

COMPARATIVE OSTEOLOGY

Having outlined the main morpholog-ical features of the most generalized rep-resentative, i.e., *Ectodus*, we can consid-
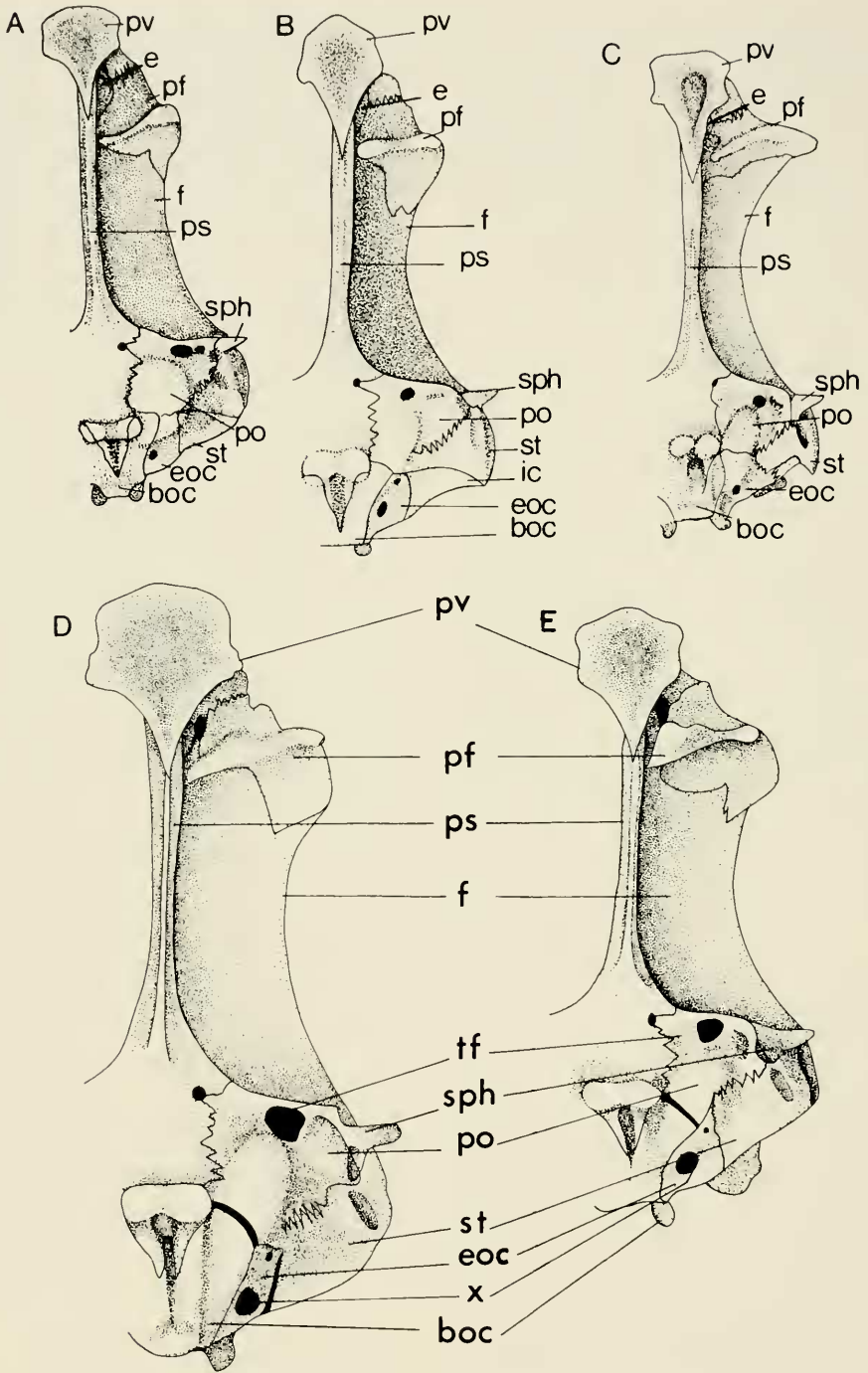
Figure 3.   Ventral aspect of the left half of the neurocranium. A, *Ectodus descampsi*; B, *Lestradea perspicax*; C, *Asprotilapia leptura*; D, *Ophthalmotilapia ventralis*; E, *Ophthalmotilapia boops*.

er the anatomy of the other members of the assemblage. The comparative description will not be a comprehensive one. Instead, emphasis will be placed on: (1) features that deviate from those found in *Ectodus*; (2) structural specializations characterizing each genus; and (3) morphological elements which can be used to interrelate the different lineages on a sister group basis.

Neurocranium (Figs. 1, 2, 3). The neurocranium of *Lestradea* is identical to that of *Ectodus* except for a somewhat shorter ethmovomerine complex (Fig. 2B). In *Cunningtonia* the ethmovomerine complex is distinctly shorter, while the basioccipital is excluded from the pharyngeal apophysis (Fig. 2C). The ethmovomerine region in *Ophthalmotilapia* is greatly abbreviated so that the prefrontal is vertically oriented. The neurocrania of *Ophthalmotilapia* and *Ophthalmochromis* resemble each other very closely, both having enlarged sensory canals and foramina. As in *Cunningtonia*, the basioccipital is excluded from the pharyngeal apophysis (Fig. 3C,D,E). However, in *Ophthalmochromis* the abbreviation of the ethmovomerine region is much less pronounced, while the enlargement of sensory canals and foramina is much greater. *Ophthalmochromis* and *Ophthalmotilapia* differ in the orientation of the ventral process of the basisphenoid, being vertical in the latter and oblique in the former (Fig. 2:bs). The most specialized neurocranium is represented in *Asprotilapia*: the ethmovomerine region is elongate with the ethmoid in an almost horizontal position; the lateral ethmoids are enlarged, forming pronounced preorbital processes; the interorbital width is much reduced; the orbit is greatly enlarged; and the sensory canals and foramina are reduced in size.

Opercular apparatus (Fig. 5). The opercular apparatus of all members of this lineage conforms with that of *Ectodus*.

Suspensory apparatus (Fig. 4). The description of the suspensory apparatus for *Ectodus* also applies to the other five genera of this lineage. However, in *Cunningtonia* the palatine is further specialized by the development of a posteriorly directed slender process at the posterodorsal corner. Although the vertical depth of the suspensorium at the level of the metapterygoid is characteristically shallow for all members of this lineage, the feature is least developed in *Ophthalmotilapia* and most pronounced in *Cunningtonia*. *Cunningtonia* also possesses a very elongate and nearly horizontal symplectic, and the horizontal limb of the preoperculum is longer than the vertical one. In *Ectodus* the horizontal and vertical limbs of the preoperculum are of equal length, while in *Asprotilapia, Lestradea, Ophthalmochromis,* and *Ophthalmotilapia* the horizontal limb of the preoperculum is the shorter one. The sensory canals and pores of the preoperculum are enlarged in *Ophthalmochromis* and *Ophthalmotilapia*.

Jaw apparatus (Fig. 4). As discussed above, the mandible of *Ectodus* is specialized in having an extensive shelflike adductor fossa in the anguloarticular and a laterally expanded ascending process of the dentary. The mandible of *Lestradea, Cunningtonia, Ophthalmochromis,* and *Ophthalmotilapia* exhibits a more generalized configuration with very restricted adductor fossae. The most specialized features are found in the mandible of *Asprotilapia*: the lower jaw is elongate and quite slender, with a drastic reduction in the depth of the unit; the large ascending processes of the dentary and articular are widely separated and form the bulk of the mandible. Morphologically, the premaxillae and maxillae in this lineage are very uniform, resembling those of *Ectodus*. But in *Lestradea* the body of the maxilla is stout, being only as long as the neck and associated condyles, and having a pronounced posteriorly directed postmaxillary process. In general, the ascending processes are shorter than in *Ecto-*
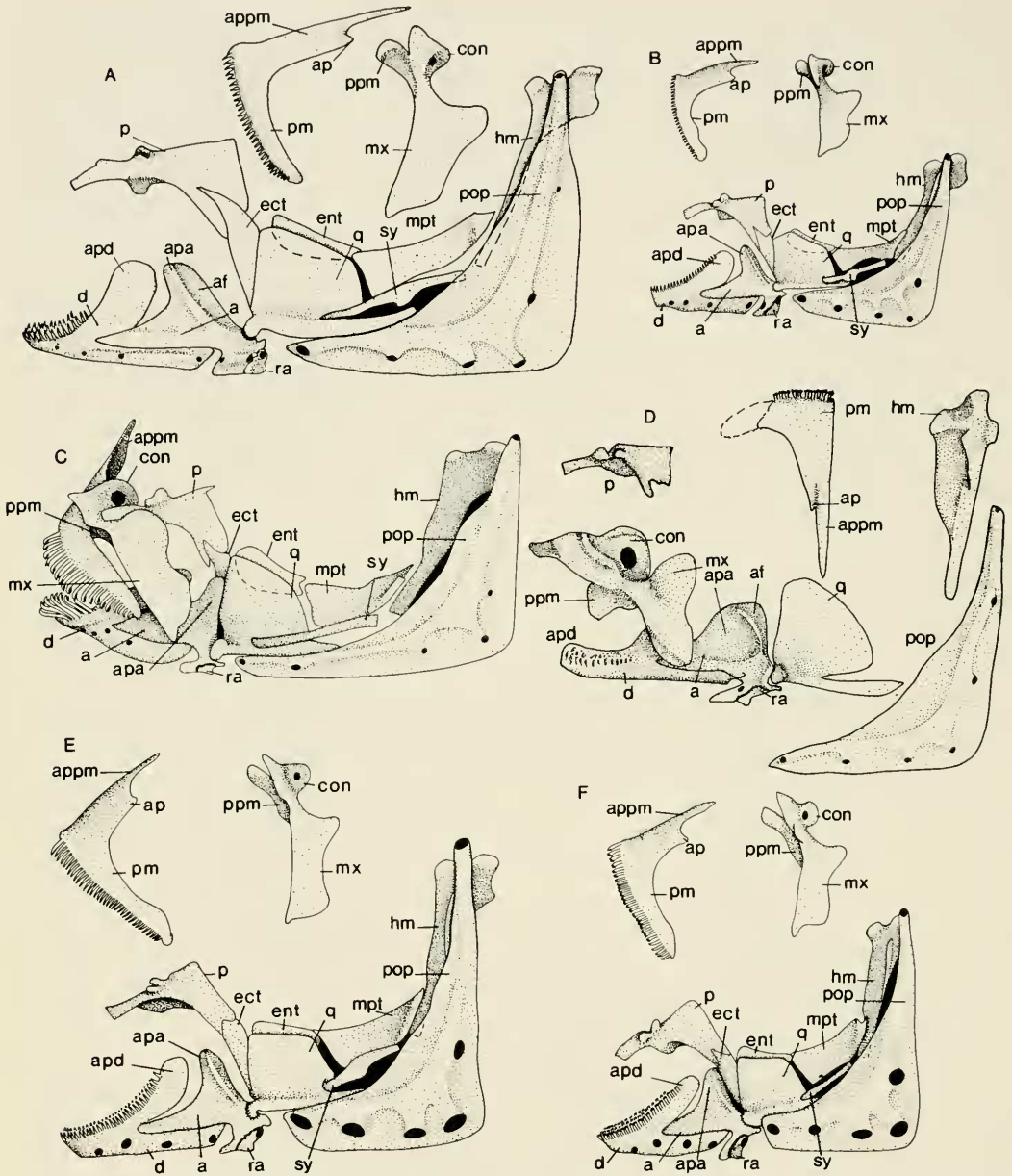
Figure 4.   Lateral aspects of the suspensorium, mandible, and upper jaw. A, *Ectodus descampsi*; B, *Lestradea perspicax*; C, *Cunningtonia longiventralis*; D, *Asprotilapia leptura*, in which only parts of the suspensorium are depicted, since the elements have been disarticulated; E, *Ophthalmotilapia ventralis*; F, *Ophthalmotilapia boops*.

dus. However, both the premaxilla and maxilla in *Asprotilapia* (Fig. 4D) exhibit several unique specializations. In the premaxilla, the articular process is re-

duced and shifted into a more forward position. The shape of the shortened maxilla deviates greatly from that of other cichlids. The greatly enlarged cranial
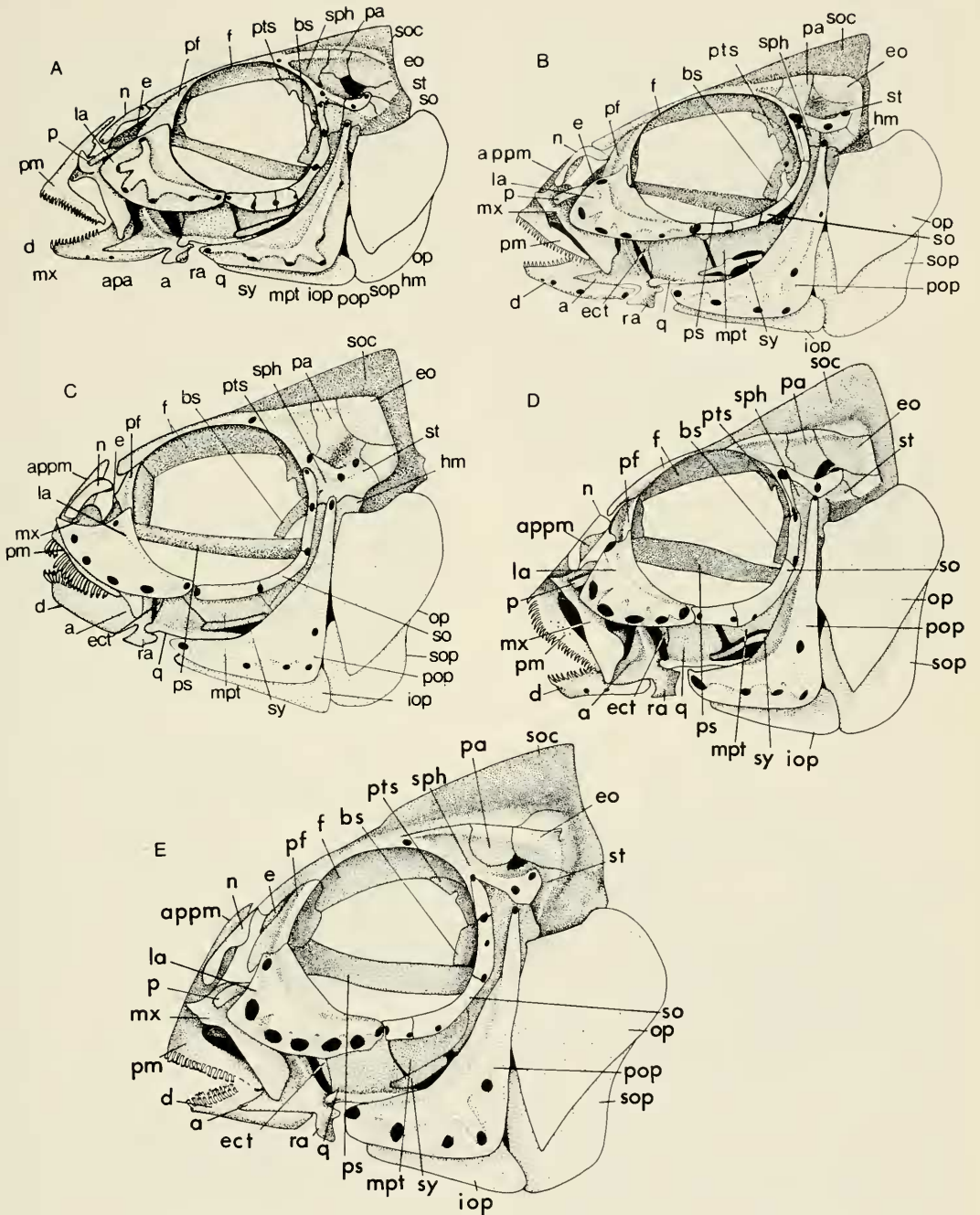
Figure 5. Lateral aspect of the skull. A, *Ectodus descampsi*; B, *Lestradea perspicax*; C, *Cunningtonia longiventralis*; D, *Ophthalmotilapia ventralis*; E, *Ophthalmotilapia boops*.
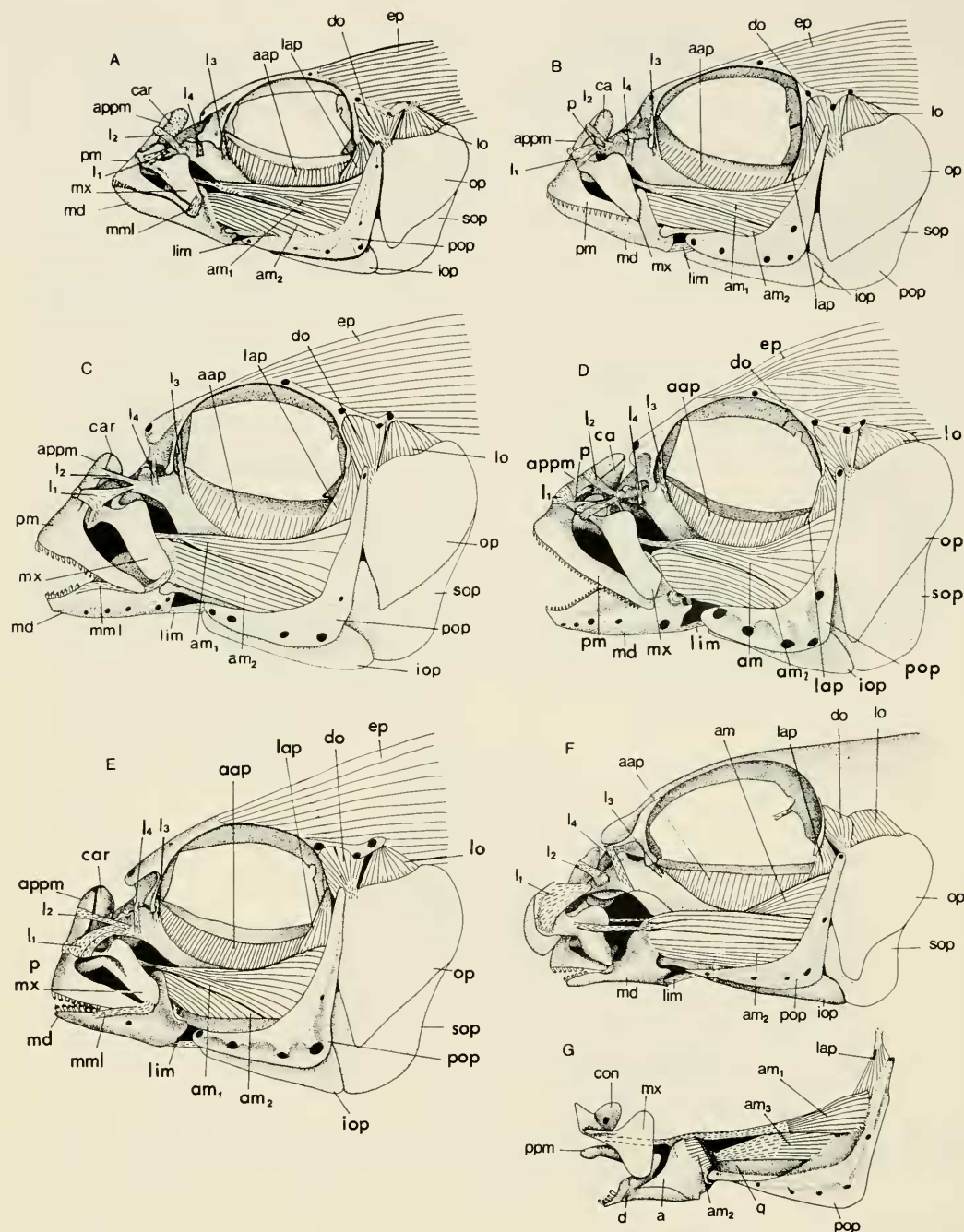
Figure 6.   Lateral aspect of the cephalic musculature after removal of the lacrimal, circumorbitals, and eyes. A, *Ectodus descampsi*; B, *Lestradea perspicax*; C, *Cunningtonia longiventralis*; D, *Ophthalmotilapia ventralis*; E, *Ophthalmotilapia boops*; F, *Asprotilapia leptura*; G, deeper dissection of the adductor mandibulae complex after removal of part A₂ in *Asprotilapia*.

condyle and premaxillary process consti-
tute the bulk of the bone, with its dorsal
extremity directed anteriorly as a flat-
tened process. The angle between the
body of the maxilla and the part bearing
the cranial condyle and premaxillary pro-
cess is more acute than that of other
members of the lineage.

Dentition. Much of cichlid classifica-
tion and phylogeny has been based sole-
ly on dental characters. In this lineage
dental characters are of little value in es-
tablishing phyletic relationships at the
generic level, because the polarity of
character transformation is not known,
and intraspecific and ontogenetic plastic-
ity further complicates the use of dental
characters. No new information is added
here to our already extensive knowledge
on the teeth of members of this lineage
(Poll, 1943; Poll and Matthes, 1962). In
Ectodus descampsi the teeth are conical
and arranged in two to three rows in such
a fashion that the outer rows on the lower
jaw are directed outward. *Lestradea per-
spicax perspicax,* a subspecies from the
northern half of Lake Tanganyika, pos-
sesses conical teeth arranged in three to
four rows. The teeth of the outer row are
much larger and are directed outward. In
juveniles of *L. perspicax stappersi* the
teeth are invariably tricuspid, while in
the adult all teeth can become conical.
Cunningtonia, Ophthalmochromis, and
Ophthalmotilapia have teeth with long
flexible stalks, giving them a mobile na-
ture, which is regarded as an adaptation
to raking and scraping algae off irregular
rock surfaces. In *Cunningtonia* the tri-
cuspid teeth are numerous, forming a
broad band in each jaw. Characteristical-
ly, the distal end of each tooth is bent
backwards rather sharply. In *Ophthal-
motilapia* most teeth are tricuspid
throughout the life history of the fish, ex-
cept for the conical ones toward the outer
corners of the jaws. It is remarkable that
the dental patterns in the subspecies of
Lestradea closely parallel those in the
subspecies of *Ophthalmochromis.*
Ophthalmochromis ventralis ventralis is

a conical-toothed form, geographically
restricted to the northern half of Lake
Tanganyika. In the southern subspecies,
*Ophthalmochromis ventralis heterodon-
tus,* the juveniles have tricuspid teeth,
while later in development a mixed den-
tition of tricuspid and conical teeth ap-
pears. *Asprotilapia* has small teeth with
very long slender stalks and expanded
tricuspid crowns arranged in two rows.

COMPARATIVE MYOLOGY

The lateral head musculature in mem-
bers of this lineage is relatively uniform
(Figs. 6, 7, 8). The description given for
Ectodus also applies to other members of
the lineage except for *Asprotilapia,*
which exhibits many unique specializa-
tions in the lateral head musculature. In
Asprotilapia (Fig. 6F,G) the elongate ad-
ductor mandibulae part A_2 is the domi-
nant muscle occupying the greater part of
the cheek region. From their origin on
the preoperculum, the fibers run parallel
to insert on the extensive adductor fossa
of the mandible. Part A_1 of the adductor
mandibulae complex in *Asprotilapia* is
a small muscle originating from the pre-
operculum and symplectic processes of
the hyomandibula; its fibers insert on a
tendon at a point about halfway between
origin and insertion. Thus the tendon of
part A_1 is exceptionally long; just beyond
the ascending process of the articular it
gives off a ventral branch which merges
with the tendon of the intramandibular
(A_w) part of the adductor mandibulae
complex. The A_1 tendon inserts on the
medial aspect of the maxilla in the area
between the cranial condyle and premax-
illary process. The adductor mandibulae
complex of *Lestradea, Cunningtonia,
Ophthalmochromis,* and *Ophthalmoti-
lapia* deviates from that of *Ectodus* in the
dominance of the A_1 part. Both in cross-
sectional area and in volume, the A_1 is
the largest component of the complex
(Fig. 6).

The configuration of the remaining lat-
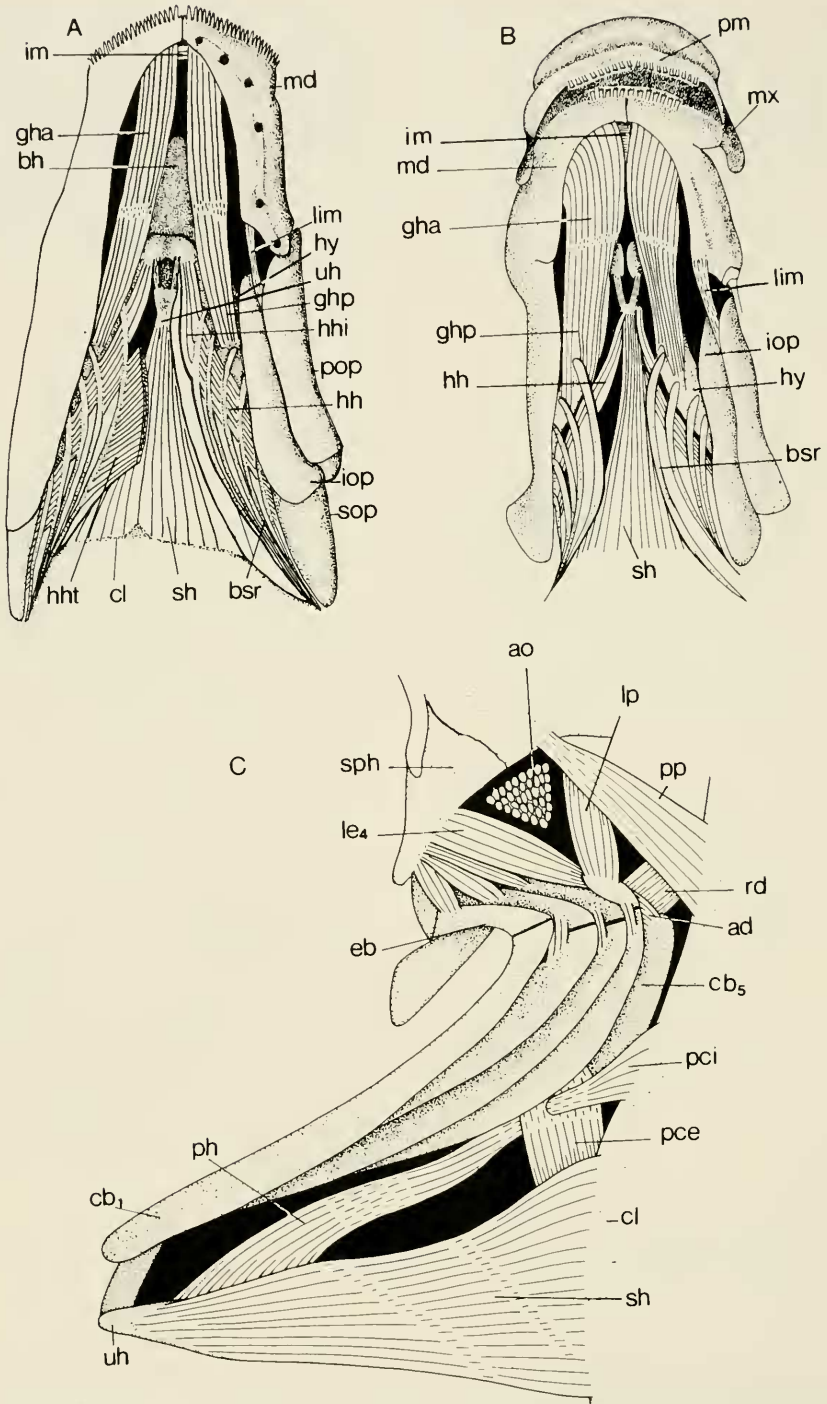eral head muscles and the ventral head

Figure 7.   Ventral aspect of the ventral cephalic musculature with the hyohyoideus transversus partially or in B, entirely removed. A, *Ectodus descampsi*; B, *Asprotilapia leptura*; C, lateral view of the branchial musculature after removal of the gills and mucous membranes in *Ophthalmotilapia nasutus*.

muscles in all members of this lineage conforms with that of *Ectodus* (Fig. 6).

In general, the branchial musculature of members of this lineage resembles that of *Ectodus* (Figs. 7, 8). In *Asprotilapia* the transversus dorsalis anterior muscles have been reduced to only one head, running between the 2nd pharyngobranchials (Fig. 8C:tda). *Ophthalmotilapia* exhibits two specializations in the dorsal branchial musculature: both the obliquus dorsalis and retractor dorsalis are greatly enlarged and are subdivided into two distinct heads (Fig. 8D:od,rd).

PHYLETIC ANALYSIS

Although an in depth study on phyletic relationships is not yet available, it is generally accepted that the endemic lacustrine cichlids of Lake Tanganyika have been derived from several unrelated fluviatile lineages. The fluviatile genera "*Tilapia*," *Tylochromis*, "*Haplochromis*," and *Lamprologus* are considered the primitive sister lineages of the many derived lineages of endemic cichlids in Lake Tanganyika (e.g., Regan, 1920; Fryer and Iles, 1972). Unfortunately, no attempts have been made to interrelate the different lineages within Lake Tanganyika on a sister group basis. Since the phyletic relationships of the lacustrine lineages are still poorly known, the determination of their sister group interrelationships with the more generalized fluviatile lineages will be postponed until a much broader data base is available. Without the information on the relationships of the lacustrine species and their respective fluviatile sister lineages, it is impossible to make precise outgroup comparisons. Despite these limitations, it is possible to construct a classification from which a theory of relationships is recoverable. Clearly its precision and efficiency can be improved, but that must await a phyletic analysis of fluviatile taxa.

In this phyletic analysis comparisons have been made between the lacustrine assemblage *Asprotilapia, Ectodus, Lestradea, Cunningtonia, Ophthalmochromis*, and *Ophthalmotilapia* and the fluviatile taxa *Astatotilapia burtoni* and *Sarotherodon nilotica. Tylochromis, Sarotherodon, Tilapia*, and *Lamprologus* are specialized along very different lines (Liem, in prep.) and are not closely related to the *Ophthalmotilapia* lineage. Although an outgroup comparison is tentative, I have considered the morphology of *A. burtoni* to be generalized (Liem, in prep.) and therefore representative of a plesiomorphous group with which the apomorphous *Ophthalmotilapia* assemblage can be compared. In the succeeding phyletic analysis I have made the basic assumption that the morphological condition of the various structures in *Astatotilapia burtoni* and *A. elegans* represents the primitive state. Any deviations from this basic morphological configuration are considered specializations. Monophyletic lineages are then formulated on the basis of shared specialized characters.

THE *OPHTHALMOTILAPIA* ASSEMBLAGE AS A MONOPHYLETIC LINEAGE

A comparison of the osteology and myology of all cichlid genera of Lake Tanganyika and the four fluviatile species *Sarotherodon nilotica, Astatotilapia burtoni, Tylochromis microlepis*, and *Lamprologus congolensis* has resulted in the identification of a suite of eight derived characters shared by *Asprotilapia, Ectodus, Lestradea, Cunningtonia, Ophthalmochromis*, and *Ophthalmotilapia*. This group of genera will be referred to as OA (*Ophthalmotilapia* Assemblage) in the following discussion.

The entopterygoid is separated from the palatine in the OA (Fig. 4:ent). In generalized cichlids the entopterygoid is attached to the posterior margin of the body of the palatine (Goedel, 1974; Vandewalle, 1972; Liem and Osse, 1975; Barel *et al.*, 1976) or the two elements abut against each other. A similar connection is also present in several special-
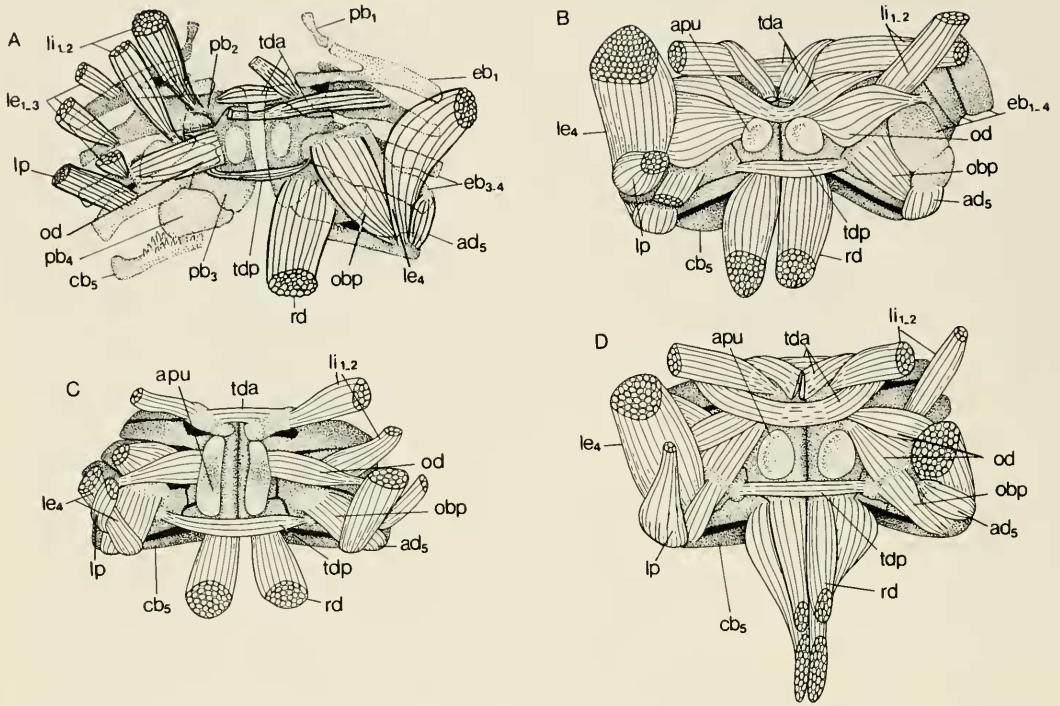
Figure 8.   Dorsal aspect of the branchial musculature. A, *Ectodus descampsi,* in which the dissection has been carried out in greater detail to show the precise insertions and origins of the muscles; B, *Lestradea perspicax*; C, *Asprotilapia leptura*; D, *Ophthalmotilapia boops.*

ized lineages of Lake Tanganyika, such as the herbivores (e.g., *Simochromis* and *Petrochromis*), piscivores (Liem, 1978), scale eaters (Liem and Stewart, 1976) and invertebrate pickers (Liem, 1979). Separation of the palatine and the entopterygoid (Fig. 4:ent,p) is considered as a derived character state. This specialization also occurs in *Xenotilapia* (Liem and Osse, 1975), *Aulonocranus, Callochromis,* and *Cardiopharynx* indicating the possibility that these genera are related to the OA. However, on the basis of the present data it is impossible to ascertain that *Xenotilapia, Aulonocranus, Callochromis,* and *Cardiopharynx* are members of a sister lineage of the OA.

The functional significance of the separation of the entopterygoid from the palatine remains unclear, because no correlation can be found between this specialized feature and specializations in either the mobility and shape of the suspensorium and jaws, or the morphological characteristics of the adductor mandibulae complex.

A unique specialization of the OA can be found in the palatine bone (Fig. 4E,F:p). The dorsal margin and the vertically directed posterior border of the palatine meet at a 90° angle. Because the palatine is expanded in the region of this 90° angle, it has a characteristic shape when viewed laterally (Fig. 4:p). The 90° posterodorsal angle surmounting a posterodorsal expansion of the palatine is not found in any of the other Lake Tanganyika cichlids and deviates from the condition in generalized cichlids (e.g., *Astatotilapia burtoni*, Liem and Osse, 1975; *A. elegans,* Barel *et al.,* 1976). This uniquely specialized shape of the pala-

tine is found in all members of the OA, indicating that the group may represent a monophyletic lineage.

The hyomandibula of cichlids exhibits remarkable diversity in shape and size. However, among the diverse forms one can recognize distinct themes, each of which may reflect a particular ancestry. The hyomandibula of *Astatotilapia burtoni* (Liem and Osse, 1975) and *A. elegans* (Barel *et al.*, 1976) is characteristically stout, with an expanded flange associated with the relatively short symplectic process. In *Tilapia* and *Sarotherodon* (Vandewalle, 1972; Goedel, 1974) the symplectic process is elongate and the hyomandibular flange below the anterior head is only moderately developed. Both *Lamprologus* and *Tylochromis* possess a strongly modified hyomandibula. The slender hyomandibula of all members of the OA (Fig. 4:hm) resembles that of *Tilapia,* but it has a relatively longer symplectic process, and has lost its flange. However, a reduced flange is present in *Asprotilapia.* Because the specialization of the hyomandibula in members of the OA has progressed further than in *Tilapia,* the feature is considered derived and indicative of the monophyletic nature of the group. A similarly specialized hyomandibula is found in *Xenotilapia.*

The anterior margin of the pterosphenoid in members of the OA is peculiarly notched (Fig. 2:pts). A liplike process at the base of the notch serves as the origin of a strong ligament which attaches to the eye ball. Although the notched anterior margin of the pterosphenoid and the associated ligament occurs in some other specialized cichlids, it is absent in the generalized forms. The presence of the pterosphenoid notch in all members of the OA is considered as supporting evidence for the hypothesis of monophyly of the OA.

All members of the OA possess a very shallow suspensory apparatus at the level of the metapterygoid (Fig. 4). This specialization is the result of a sharp decrease in the vertical depth of the metapterygoid, which in all generalized cichlids has a much greater vertical depth. Actually among Lake Tanganyika cichlids this specialization and the peculiar position of the ectopterygoid is characteristic of the OA assemblage.

Although the presence of a well-developed auricular process (Fig. 5:op) on the operculum occurs in several specialized cichlid groups, the character is here included in the suite of derived characters, upon which the hypothesis of monophyly of the OA is based.

Two myological specializations in the branchial musculature of all members of the OA offer further evidence for the probable monophyletic nature of the group. In sharp contrast to the condition in generalized cichlids, there is a clear reduction in the development of the transverse dorsalis muscle accompanied by a hypertrophy of the obliquus posterior muscle (Fig. 8:obp). Reduction of the transversus dorsalis and hypertrophy of the obliquus posterior have not been found in *Astatotilapia elegans* (Anker, 1978) and other groups of specialized cichlids in Lake Tanganyika. In view of this admittedly tentative evidence, the reduction of the transversus dorsalis and hypertrophied obliquus posterior are considered derived characters supporting the notion that the OA is actually monophyletic.

The OA is viewed as a monophyletic lineage (Fig. 9: cladogram of synapomorphies [1]–[30]) because its members share the following suite of characters:

(1) The entopterygoid is widely separated from the palatine.
(2) The posterior and dorsal margins of the palatine form a 90° angle.
(3) The slender hyomandibula has a long symplectic process and no or a very reduced hyomandibular flange.
(4) The anterior margin of the pterosphenoid is notched.
(5) The vertical depth of the metapterygoid is shallow.

(6) The operculum has a distinct auricular process.

(7) The transversus dorsalis is reduced.

(8) The obliquus posterior is enlarged.

No other cichlid in Lake Tanganyika possesses this suite of derived characters, although none of the above mentioned characters, with the possible exception of (2), is autapomorphic. The sister group of the *Ophthalmotilapia* lineage is still unknown. Possibly, *Xenotilapia, Callochromis,* and *Aulonocranus* may represent members of a sister group of the *Ophthalmotilapia* lineage since they do share two of the above mentioned derived characters (i.e., [1] and [3]). However, the precise relationships of this lineage to others must await more data and further analysis now in progress.

This phyletic hypothesis for the existence of an *Ophthalmotilapia* lineage differs from the previous hypotheses (Fryer and Iles, 1972, and Regan, 1920) by the inclusion of *Ectodus*. In the previous schemes, *Ectodus* has been regarded as a derivative of a *"Haplochromis"* or *"Haplochromis*-like" ancestor, while the other members of the *Ophthalmotilapia* lineage were seen as derivatives of "one or more unknown ancestors," which are not related to *"Haplochromis."* Unfortunately the inferred relationships of the relevant genera in the previous hypotheses have been presented with virtually no documentation, and were not based on Hennigian methodology.

Phyletic Relationships of Members of the Ophthalmotilapia Lineage

The proposed phyletic relationships are depicted in the cladogram in Fig. 9. Two major lineages are recognized: one contains the monotypic genus *Asprotilapia*, and the second lineage contains the five remaining genera. The following discussion deals first with the synapomorphies for the entire complex, and then with those derived characters that distinguish subunits of decreasing levels of universality within the assemblage.

Asprotilapia represents a very specialized lineage, with six autapomorphic characters:

(9) The elongate, slender mandible has an expanded adductor fossa (Fig. 9:9) serving as the insertion site for the adductor mandibulae part A_2 (Fig. 6F,G).

(10) The posterior head of the transversus dorsalis anterior is absent (Figs. 9:10, 8C:tda).

(11) The lateral ethmoids are greatly enlarged (Figs. 1C, 3C:pf).

(12) The interorbital width of the neurocranium is drastically reduced (Fig. 1C).

(13) The reduced articular process of the premaxilla is in a more forward position (Fig. 4D:ap).

(14) The greatly enlarged cranial condyle and the premaxillary process constitute the bulk of the maxilla (Fig. 4D:cc,pmp).

The rare species *Asprotilapia leptura* represents a highly specialized lineage, with a very elongate body and a much attenuated caudal region. Because of the ventral mouth and the tricuspid teeth arranged in two series on both jaws, *Asprotilapia* is considered herbivorous, feeding primarily on epilithic algae.

The remaining five genera are regarded as a monophyletic group on the basis of their sharing two derived characters:

(15) Anteriorly the enlarged lachrimal is differentiated into a distinct process (Figs. 9:15, 5:la). The blunt process is directed anteroventrally, except in *Cunningtonia* in which it is directed anterodorsally.

(16) The adductor mandibulae part A_1 has become the dominant component of the adductor mandibulae complex (Fig. 6:am$_1$). Its cross-sectional area surpasses that of the other parts. The origin from the preoperculum has expanded ventrally
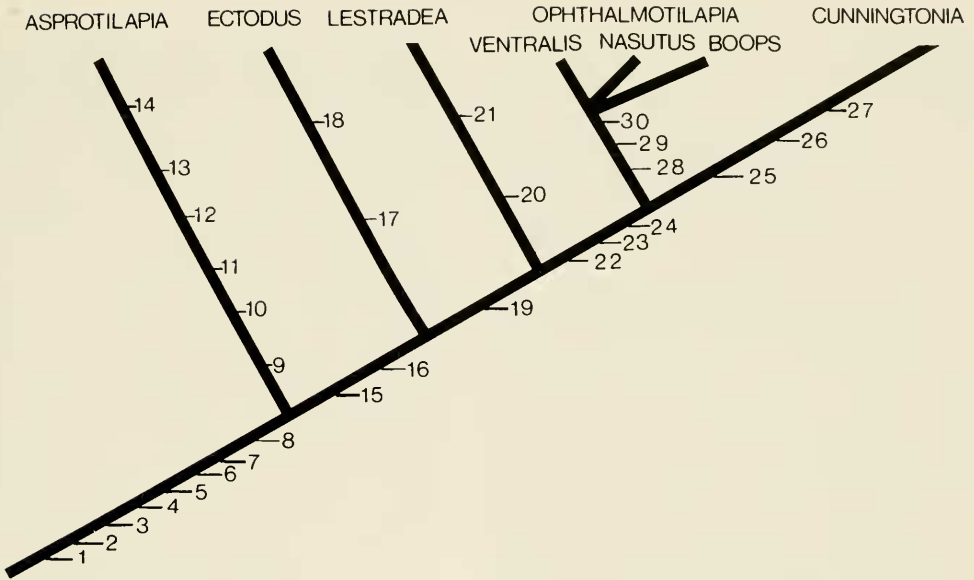
ASPROTILAPIA   ECTODUS   LESTRADEA   OPHTHALMOTILAPIA   CUNNINGTONIA

VENTRALIS NASUTUS BOOPS

[Cladogram figure with branch labels: 14, 13, 12, 11, 10, 9, 8, 7, 6, 5, 4, 3, 2, 1 on Asprotilapia lineage; 18, 17, 16, 15 for Ectodus; 21, 20, 19 for Lestradea; 30, 29, 28, 25, 24, 23, 22 for Ophthalmotilapia; 27, 26 for Cunningtonia]

Figure 9. Proposed cladogram depicting the phylogenetic relationships of the *Ophthalmotilapia* lineage on the basis of the following synapomorphies: (1) entopterygoid separated from palatine; (2) posterior and dorsal margins of palatine form a 90° angle; (3) slender hyomandibula with long symplectic process and reduced hyomandibular flange; (4) anterior margin of pterosphenoid notched; (5) vertical depth of metapterygoid shallow; (6) operculum with auricular process; (7) transversus dorsalis muscle reduced; (8) obliquus posterior muscle enlarged; (9) elongate, slender mandible with expanded adductor fossa; (10) transversus dorsalis anterior absent; (11) prefrontals greatly enlarged; (12) interorbital width greatly reduced; (13) reduced articular process of premaxilla in forward position; (14) cranial condyle and premaxillary process of maxilla greatly enlarged; (15) lacrimal enlarged with a distinct anterior process and elaborate sensory system; (16) adductor mandibulae part A_1 is dominant; (17) saccular bulla enlarged; (18) horizontal and vertical limbs of preoperculum of equal length; (19) elongate gut which is at least 2.5 times the fish's standard length; (20) edentulous anterior process of the lower pharyngeal jaw is only half as long as the toothed part; (21) stout body of maxilla with prominent postmaxillary process; (22) jaw teeth mobile with long stalks; (23) first pelvic fin ray is greatly elongate; (24) straight vertical limb of preoperculum forms a 90° angle with horizontal limb; (25) symplectic elongate; (26) a spinelike process at junction of dorsal and posterior margins of palatine; (27) long-stalked tricuspid jaw teeth with posteriorly recurved crowns; (28) distal end of elongate first ray uniquely bifid and widened into spatulae; (29) trend toward enlarged sensory canals and pores; (30) hypertrophied retractor dorsalis muscle subdivided into two distinct heads.

at the expense of the adductor mandibulae part A_2.

Ectodus inhabits shallow waters of sandy areas, feeding on a mixed diet of insect larvae, crustaceans, and filamentous algae. According to the present phylogenetic hypothesis, *Ectodus* represents the most primitive of the *Ophthalmotilapia* lineage. Two autapomorphies distinguish *Ectodus* from the other genera:

(17) The saccular bulla is greatly enlarged (Figs. 2, 3).
(18) The horizontal and vertical limbs of the preoperculum are of equal length (Figs. 4, 5:pop).

The next monophyletic subunit is composed of *Lestradea, Ophthalmotilapia, Ophthalmochromis,* and *Cunningtonia,* which all share one notable feature:

(19) The gut is elongate and is at least 2.5 times the fish's standard length.

Lestradea possesses a gut which is 2.5–4 times the standard length. In *Ophthalmotilapia* and *Ophthalmochromis* the gut measures 3–3.5 times the standard length. The longest gastrointestinal tract is that of *Cunningtonia*, measuring 5–6 times the fish's standard length. The relative increase in the length of the digestive tract is correlated with an increased emphasis on a herbivorous diet.

Within this subunit, *Lestradea* can be

distinguished by two autapomorphic characters:

(20) The edentulous anterior process of the lower pharyngeal jaw is only half as long as the toothed part.
(21) The body of the maxilla is stout and has a prominent postmaxillary process (Fig. 4).

Cunningtonia, Ophthalmochromis, and *Ophthalmotilapia* form a distinct subunit sharing three specialized characters:

(22) The jaw teeth have long stalks and are mobile.
(23) The first pelvic fin ray is greatly elongate.
(24) The posterior margin of the vertical limb of the preoperculum is straight and forms a 90° angle with that of the horizontal limb (Fig. 4).

Within this monophyletic subunit, *Cunningtonia* possesses three autapomorphic features:

(25) The symplectic is very elongate, lengthening the suspensorium (Fig. 4:sy).
(26) At the 90° junction of the dorsal and posterior margins of the palatine is a spinelike process directed dorsoposteriorly (Fig. 4:p).
(27) The long-stalked tricuspid jaw teeth have posteriorly recurved crowns (Fig. 6).

Finally, the close relationship of *Ophthalmochromis* and *Ophthalmotilapia* can be established on the basis of three derived characters:

(28) The distal end of the very elongate first ray of each pelvic fin in the male is uniquely bifid and widened into spatulae.
(29) All members of this subunit show a trend toward enlargement of the sensory canals and pores of the head (Figs. 1, 2, 5).
(30) The hypertrophied retractor dorsalis is subdivided into two distinct heads (Fig. 8:rd).

The genus *Ophthalmochromis* was established by Poll (1956) on the basis of *O. ventralis,* its type species possessing conical teeth in adults as well as juveniles. *Ophthalmotilapia boops,* on the other hand, has mainly tricuspid teeth, although conical teeth are present on the posterolateral corner of the jaws. The neurocranium of *O. boops* has a shorter ethmovomerine region and a steeper ethmovomerine slope than that of *Ophthalmochromis ventralis.* However, the condition with respect to the ethmovomerine region in the skull of *Ophthalmochromis nasutus* is intermediate between that of *boops* and *ventralis.* The validity of *Ophthalmochromis* and *Ophthalmotilapia* as distinct genera is questionable.

Originally the distinction between *Ophthalmochromis* and *Ophthalmotilapia* was based on morphological gaps in the general and skull morphology. With the discovery of *Ophthalmochromis nasutus,* the few morphological gaps of characters in the skulls of *ventralis* and *boops* are bridged. *Ophthalmochromis nasutus* has an ethmovomerine slope intermediate between those of *ventralis* and *boops.* The subtle differences in the decurvature of the skull anteriorly between *Ophthalmochromis* and *Ophthalmotilapia* are well within the range found intragenerically in *Perissodus* (Liem and Stewart, 1976). In the related genus *Lestradea,* the contrast between tricuspid and conical teeth has been interpreted to indicate a difference at the subspecies level for, respectively, *L. perspicax stappersi* and *L. perspicax perspicax.* In *Lestradea* tooth shape changes ontogenetically from tricuspid to bicuspid and conical. In *ventralis, nasutus,* and *boops* geographical variation has been demonstrated very convincingly (Poll and Matthes, 1962). Conical teeth do occur in all species, even though in *boops* the tricuspid form is dominant. In view of the fact that tooth form in some members of this lineage can change drastically from tricuspid to conical during ontogeny, and that conical teeth actually

occur in all forms varying only in relative abundance, the presumed "morphological gap" between *ventralis* and *nasutus* on the one hand, and *boops* on the other hand, is nonexistent and does not justify the recognition of two genera.

More importantly, the phylogenetic relationships as depicted in Fig. 9 indicate that *ventralis*, *nasutus*, and *boops* share a recent common ancestor not shared by any of the other taxa. I propose, therefore, that *Ophthalmotilapia* and *Ophthalmochromis* be considered synonyms. The name *Ophthalmotilapia* established by Boulenger in 1901 has priority over *Ophthalmochromis* (Poll, 1956).

"ADAPTIVE RADIATION" OF THE OPHTHALMOTILAPIA LINEAGE

Once the phyletic nature and relationships of the *Ophthalmotilapia* lineage have been established, a more meaningful statement can be made concerning their adaptive radiation.

Unlike most cichlid lineages, the radiation in the *Ophthalmotilapia* lineage especially has involved behavioral patterns in courtship and specific recognition signals, although the feeding apparatus does exhibit some morphological diversity. All are oral brooders, but in *Cunningtonia* and *Ophthalmotilapia* the pelvic fins of the males are drawn out into long slender filaments whose tips reach posteriorly to the margin of the anal fin and terminate in brightly colored spots which function not only for species recognition, but probably also as egg dummies (Fryer and Iles, 1972: 110, 121). The strikingly colored tips of the elongated pelvic fins play an important role in specific, and, thus inevitably, in sex recognition in the complex communities where *Cunningtonia* and *Ophthalmotilapia* occur. Both *Cunningtonia* and *Ophthalmotilapia* produce only a few eggs, measuring 3.5–4 mm in diameter. Egg collecting precedes fertilization. *Ectodus*, the most primitive member of the lineage, and *Lestradea* produce larger clutches (20–30) of smaller eggs (2 mm) and lack the specialized brilliantly colored tips on the elongate pelvic fins. The males of *Lestradea* and *Ectodus* possess different specific recognition signals, and their courtship behaviors differ from those of *Cunningtonia* and *Ophthalmochromis*. In *Lestradea* and *Ectodus* egg laying, fertilization, and collection by the female take place rapidly in that sequence. The courship behavior of *Asprotilapia* is unknown.

Members of the *Ophthalmotilapia* lineage occupy three types of habitat. Generally, *Asprotilapia*, *Cunningtonia*, and *Ophthalmotilapia* inhabit the offshore margins of the shallow, rocky littoral adjacent to the sandy bottom. *O. ventralis* often penetrates to greater depths of up to 5 m. *Lestradea* inhabits shallow areas with both sandy and rocky bottoms. *L. perspicax stappersi* is common at greater depths down to 50 m. The littoral habitat of *Ectodus* is much narrower, being confined to the shallow waters with sandy bottoms. Except for *Ectodus*, all members of the *Ophthalmotilapia* lineage are not restricted to a particular habitat but move freely between habitats with hard and soft bottoms. The absence of strong habitat restriction means the crossing of "alien" habitats whether or not conditions are adverse. As a result, a spectrum of food resources is exploited. Judging from the anatomy, stomach contents, and behavior in the laboratory, members of the *Ophthalmotilapia* lineage possess an extensive feeding repertoire. Thus the feeding pattern exhibited by the *Ophthalmotilapia* lineage resembles that of other cichlids in which increased functional and morphological differences in the trophic apparatus (dentition, jaw structure, skull morphology, and pharyngeal myology) do not necessarily lead to a greater separation on the food axis (Liem, 1980).

The comparative anatomical and phylogenetic data presented in this study reinforces the paradox (Liem, 1980; Greenwood, in prep.) that the morpho-

logically and phylogenetically most specialized cichlid taxa are not only remarkable specialists but also jacks-of-all-trades. How the morphological radiation of the feeding apparatus has evolved remains a major problem in understanding the causal factors underlying the spectacular diversifications in the cichlid trophic structures. If specialists are simultaneously jacks-of-all-trades, they defy the commonly accepted ecological notion that broadening the range of usable resources prevents species from specializing on individual types. So far, most studies have attempted to correlate the morphological diversity in the feeding apparatus of cichlids with adaptation and therefore fitness. However, Carson (1970) and Fryer (1977) have suggested that speciation and adaptation are not necessarily synchronous processes. Carson has offered evidence that in Hawaiian drosophilids speciation may have preceded adaptation.

Although there is no doubt that the *Ophthalmotilapia* lineage has undergone extensive morphological radiation in both skull structure and dentition, the data on morphology, function, trophic ecology, and behavior of this and other cichlid lineages (Liem, 1980) have failed to establish unequivocally that the morphological radiation is also adaptive.

ACKNOWLEDGMENTS

ABBREVIATIONS

a: anguloarticular
aap: adductor arcus palatini
ad: adductor branchialis
ad_5: fifth adductor
af: adductor fossa
am_1: adductor mandibulae pars A_1
am_2: adductor mandibulae pars A_2
am_3: adductor mandibulae pars A_3
ao: adductor operculi
ap: articular process
apa: ascending process of articular
apd: ascending process of dentary (coronoid)
appm: ascending process of premaxilla
apu: apophysis of upper pharyngeal jaw
bh: basihyal
boc: basioccipital
bs: basisphenoid
bsr: branchiostegal ray
ca: rostral cartilage
car: rostral cartilage
cb_1: first ceratobranchial
cb_5: fifth ceratobranchial (lower pharyngeal jaw)
cl: cleithrum
con: cranial condyle
d: dentary
do: dilatator operculi
e: ethmoid
eb: epibranchial
eb_1: first epibranchial
eb_{3-4}: third and fourth epibranchial
ect: ectopterygoid
ent: entopterygoid
eo: epiotic
eoc: exoccipital
ep: epaxial muscles
f: frontal
gha: geniohyoideus anterior
ghp: geniohyoideus posterior
hh: hyohyoideus
hhi: hyohyoideus inferior
hhs: hyohyoideus superior
hht: hyohyoideus transversus
hm: hyomandibula
hy: hyoid
ic: intercalar
im: intermandibularis
iop: interoperculum
la: lacrimal
l_1: palatomaxillary ligament

l₂: palatopalatine ligament
l₃: craniopalatine ligament
l₄: ethmopalatine ligament
lap: levator arcus palatini
le₄: fourth levator externus
li₁₋₂: first and second levator internus
lim: interoperculomandibular ligament
lo: levator operculi
lp: levator posterior
md: mandible
mml: medial mandibular ligament
mpt: metapterygoid
mx: maxilla
n: nasal
obp: obliquus posterior
od: obliquus dorsalis
op: operculum
p: palatine
pa: parietal
pb₂: second pharyngobranchial
pb₃: third pharyngobranchial
pb₄: fourth pharyngobranchial
pce: pharyngocleithralis externus
pci: pharyngocleithralis internus
pf: lateral ethmoid complex
ph: pharyngohyoideus
pm: premaxilla
pop: preoperculum
pp: postmaxillary process of maxilla
ppm: protractor pectoralis
ps: parasphenoid
pts: pterosphenoid
pv: vomer
q: quadrate
ra: retroarticular
rd: retractor dorsalis
rf: rostral fossa
sh: sternohyoideus
so: circumorbital
soc: supraoccipital
sop: suboperculum
sph: sphenotic
st: pterotic (supratemporal)
sy: symplectic
tda: transversus dorsalis anterior
tdp: transversus dorsalis posterior
tf: trigeminofacialis chamber
uh: urohyal
x: foramen of vagus nerve

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